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DIVERSIDADE BETA TAXONÔMICA E FUNCIONAL DOS PEIXES DE ÁGUA DOCE DO BRASIL

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DIVERSIDADE BETA TAXONÔMICA E FUNCIONAL DOS PEIXES DE ÁGUA DOCE DO BRASIL

Dissertação apresentada ao Programa de Pós Graduação em Ecologia e Conservação da Universidade Federal de Sergipe, como requisito para obtenção de título de Mestre em Ecologia.

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por

ISAAC TRINDADE SANTOS

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal de Sergipe, como parte dos requisitos exigidos para a obtenção do título de Mestre em Ecologia e Conservação.

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“Imagination is more important than knowledge. For knowledge is limited to all we now know and understand, while imagination embraces the entire world, and all there ever will be to know and understand.”

Albert Einstein

RESUMO

Na primeira parte deste trabalho foi avaliada a relação entre as diversidades taxonômica e funcional, alfa e beta (TβD and FβD), dos peixes de nadadeira raiada (Actinopterygii) de água doce do Brasil, em três escalas diferentes. Avaliou-se a contribuição dos componentes da β-div – 'turnover' (substituição de espécies entre comunidades) e 'nestedness', ou aninhamento, (perda de espécies) – para os padrões observados, e se eles são influenciados por processos estocásticos ou determinísticos. Enquanto TβD teve altas taxas de 'turnover' (de 93 para 98%), FβD possuiu uma maior contribuição do aninhamento (70 - 80%). Os padrões de TβD foi maior do que o esperado ao acaso. Além disso, filtros ambientais e interações bióticas desempenham um papel maior para a formação e manutenção dos padrões de diversidade dos peixes de nadadeiras raiadas primários nos Neotrópicos. Na segunda parte deste trabalho avaliou-se como os padrões de beta diversidade são influenciados por ações humanas. Utilizando o 'desastre da barragem de Bento Rodrigues', na Bacia do Rio Doce como um modelo de caso, nós avaliamos as possíveis consequências de diferentes níveis de extinções locais de espécies para a β-div regional e riqueza funcional entre seis bacias vizinhas. Uma maior contribuição do nestedness (13-19%), levou a um aumento nos padrões de diversidade beta: de 0,75 para 081 (índice de dissimilaridade de Sørensen). A riqueza functional da Bacia do Doce também diminui de 69-36%. Graças ao padrão regional de compartilhamento de espécies entre bacias, as possíveis consequências das extinções de peixes incluem a diminuição na contribuição do turnover (87-81%). O desastre causou mudanças substanciais nos padrões regionais de β-div e riqueza funcional, devido a um processo conhecido como heterogeinização subtrativa. Estes resultados podem ser relevantes para ambos, a conservação local e visão geral de como distúrbios afetam a biodiversidade.

Palavras-chave: Otto Pfaffstetter, turnover, nestedness, biogeografia, ictiofauna.

ABSTRACT

The first part of this work we assess the relationship between the taxonomic and functional alfa- and beta-diversity (TβD and FβD) in primary ray-finned fishes (Actinopterygii) from Brazil, at three different spatial scales. We assess the contribution of the components of β-div – turnover (replacement of species) and nestedness (species loss) – to the observed pattern, and whether they are driven by stochastic or deterministic processes. While TβD was ruled by high rates of turnover (from 93 to 98%), FβD had a greater contribution of nestedness (70 to 80%). Observed TβD was higher than by chance. In addition, environmental filtering and biotic interactions play a greater role for the formation and maintenance of primary ray-finned fish diversity patterns in the Neotropics. In the second part of this work we assessed how the patterns of beta diversity are affected by human actions. Taking the 'Bento Rodrigues dam disaster' at the Doce Basin as a case model, we evaluate the possible consequences of different levels of local species extinctions to the regional taxonomic β-div and functional richness across six neighbour river basins. A higher contribution of nestedness (13-19%), leaded to an increase in the pattern of beta diversity: 0.75 to 0.81 (Sørensen dissimilarity index). The functional richness from Doce Basin also decreased from 69-36%. Owing to the regional pattern of species sharing among basins, the likely consequences of fish extinctions include a decreasing trend of turnover contribution (87-81%). The disaster caused substantial changes on regional patterns of β-div and functional richness, owing to a process known as subtractive heterogenization. These findings might be relevant for both, local conservation purposes and the overview of how disturbance affect biodiversity.

Keywords: Otto Pfafstetter, turnover, nestedness, biogeography, ichthyofauna.

SUMÁRIO

RESUMO (Artigo 1)

1. Compreender o compartilhamento de espécies e seus atributos entre comunidades (diversidade beta, β-div) entre diferentes escalas espacias pode esclarescer seus determinantes ecológicos e dar suporte à sua gestão e conservação
2. Aqui, foi avaliada a relação entre as diversidades taxonômica e funcional, alfa e beta (TβD and FβD), dos peixes de nadadeira raiada (Actinopterygii) de água doce do Brasil, em três escalas diferentes. Avaliou-se a contribuição dos componentes da β-div – 'turnover' (substituição de espécies entre comunidades) e 'nestedness', ou aninhamento, (perda de espécies) – para os padrões observados, e se eles são influenciados por processos estocásticos ou determinísticos.
3. Aplicou-se o índice de dissimilaridade de Jaccard (para dois níveis de bacias hidrográficas e estados Brasileiros) para medir as contribuições do 'turnover' e aninhamento dos totais da TβD e FβD. Utilizou-se um procedimento de randomização para investigar se processos deterministicos ou estocásticos prevalecem nas comunidades de peixes primários com nadadeiras raiadas. Finalmente foi utilizado o teste de Mantel para avaliar as correlações entre os índices de diversidade taxonômicos e funcionais.
4. Enquanto TβD teve altas taxas de 'turnover' (de 93 para 98%), FβD possuiu uma maior contribuição do aninhamento (70 - 80%). Os padrões de TβD foi maior do que o esperado ao acaso. Apesar das diferentes contribuições de turnover e nestedness, existem relações siginificativas entre TβD e FβD.
5. As altas substituições de espécies entre bacias ocorrem com espécies que são funcionalmente redundantes, indicando especiação com convergência funcional. Além disso, filtros ambientais e interações bióticas desempenham um papel maior para a formação e manutenção dos padrões de diversidade dos peixes de nadadeiras raiadas primários nos Neotrópicos.

Palavras-chave: Otto Pfaffstetter, turnover, nestedness, biogeografia, ictiofauna.

Paper a ser submetido na revista Freshwater Biology (a formatação do artigo 1 segue as normas da revista).

Title

Divergent patterns of taxonomic and functional beta-diversity in Neotropical primary ray-finned fish (Actinopterygii) assemblages

Summary

1. Understanding the sharing of species and their attributes among communities (beta-diversity, β-div) across different spatial scales can shed light on their ecological drivers and support their management and conservation.

2. Here, we assess the relationship between the taxonomic and functional alfa- and beta-diversity (TβD and FβD) in primary ray-finned fishes (Actinopterygii) from the Neotropics, at three different spatial scales. We assess the contribution of the components of β-div – turnover (replacement of species) and nestedness (species loss) – to the observed pattern, and whether they are driven by stochastic or deterministic processes.

3. We employed Jaccard dissimilarity index (for two levels of hydrological basins and Brazilian states) to disentangle the contributions of turnover and nestedness for total TβD and FβD. We also used a randomization procedure to investigate whether deterministic or stochastic processes prevail in the assembling of primary ray-finned fishes communities. Finally, we used the Mantel test to assess the correlations between taxonomic and functional diversity indices.

4. While TβD was ruled by high rates of turnover (from 93 to 98%), FβD had a greater contribution of nestedness (70 to 80%). Observed TβD was higher than by chance. Despite different contributions of turnover and nestedness, significant relationships exist between TβD and FβD.

5. The high replacement of species between drainage basins occurs with species that are functionally redundant, indicating allopatric speciation with functional convergence. In addition, environmental filtering and biotic interactions play a greater role for the formation and maintenance of primary ray-finned fish diversity patterns in the Neotropics.

Keywords: Otto Pfafstetter, turnover, nestedness, biogeography, ichthyofauna.

Introduction

Understanding biodiversity patterns in space and time is essential to recover its origin and maintenance, as well as to develop management and conservations strategies. These patterns includes not only the local diversity (alpha diversity, α-div) but also the degree of variation among communities (beta diversity, β-div) within a regional scale (gamma diversity, γ-div) (Socolar *et al.*, 2016; Magurran, 2016). The terms α-div, β-div and γ-div were defined by Whittaker (1960), but only in the 1990s that these concepts became more evident (Melo *et al.*, 2011). β-div is defined as the variation of community composition among sites and they are usually explored using dissimilarity indexes, e.g. Jaccard or Sørensen (Koleff, Gaston & Lennon, 2003; Tuomisto, 2010). Dissimilarities in the composition of species assemblages can be structured in different ways, including through replacement of some species by others (known as species turnover) or through species loss where some communities are subsets of richer ones (nestedness) (Baselga & Orme, 2012).

Further than the spatial scale, the investigation of the processes responsible for structuring the biological communities requires also the embracing of multiple facets of the biodiversity (Pool, Grenouillet & Villéger, 2014). Measures of taxonomic (TD: species richness), functional (FD: morphological, physical or ecological traits of a species assembly) and phylogenetic diversity (PD: evolutionary relatedness among species) can inform different and complementary aspects of the components of biodiversity (Cardoso *et al.*, 2014). For conservation purposes, for instance, the integrated study of TD, FD and PD allows us to identify different values for conservation within and among communities, including evolutionary history and ecosystem functioning, therefore increasing the scope of conservation efforts (Pool, Grenouillet & Villéger, 2014). Assessing these biodiversity facets is also important to understand how each species of a community may respond to natural or anthropogenic disturbances (Mouillot *et al.*, 2011).

The approach of decomposing β-div into turnover and nestedness can be extended beyond taxonomic β-div (TβD), and applied to functional β-div (FβD). The amount of multidimensional functional space not shared between communities is defined as functional turnover, while the functional space shared is known as functional nestedness (Villéger, Grenouillet & Brosse, 2013). Distinct evolutionary processes affect differently these different facets of β-Div (Soininen, Lennon & Hillebrand, 2007).

In fact, it is possible to assess how deterministic processes (niche-based processes, environmental filtering, and biotic interactions) or stochastic processes (random dispersal and speciation events, ecological drift, extinction) differently shape the TβD dynamics of communities (Hubbell, 2001; Chase & Myers, 2011). Additionally, the role of FβD is associated with the functional differences or functional richness between communities and its direct relation to the ecosystem functioning (Petchey & Gaston, 2002; Mouillot *et al.*, 2013). Variations in FβD can be measured using a multidimensional functional space approach (Villéger, Mason & Mouillot, 2008).

In the context of freshwater systems, there is a large variation in the community assembly due to upstream to downstream variation within each drainage basin, causing a continuum of biotic adjustments (Vannote *et al.*, 1980) and among basins, i.e., the amount of taxonomic and functional diversity variations (Heino, 2011; Leprieur *et al.*, 2011). Freshwater systems are among the most threatened environments of the world, mainly due to the unsustainable water use for human consumption, habitat loss, overexploitation of fish stocks, and other factors such as dam construction, pollution by plastics and other residuals, dissolved oxygen depletion, invasive species and diseases (Strayer & Dudgeon, 2010; Costa & Barletta, 2016). Understanding the processes responsible for the formation of drainage basins, rivers, lakes, streams, and all biodiversity present in these heterogeneous systems plays a key role for their conservation (Albert & Reis, 2011; IUCN, 2016; Olden *et al.*, 2010). The declining rate of freshwater biodiversity has been faster than in terrestrial and marine environments and the lack of basic information and research hampers our perception of the real extension of this decline (Dudgeon *et al.*, 2006). Addressing attention for the freshwater realm is of utmost importance for food security for many communities across the globe (McIntyre, Liermann & Revenga, 2016). Out of the 33,400 fish species (49% of all vertebrates) described worldwide (Froese & Pauly, 2017; IUCN, 2016), about 16,000 species (23% of all vertebrates) are associated with freshwater environments, which represent only 0.01% of the world's total water volume (Dudgeon *et al.*, 2006; Pelayo-Villamil *et al.*, 2015). These environments harbor about 44% of the Actinopterygii (ray-fined fishes), which in turn represents one of the more speciose vertebrate taxa, with 26,891 species (Nelson, Grande & Wilson, 2016).

This study aims to investigate the relationship between taxonomic and functional diversity of ray-fined fishes in Brazil regarding their alfa- and beta-diversity, including the assessment of the proportional contribution of turnover and nestedness components

to the total TβD and FβD. We expected that for this region ichthyofaunas from distinct drainage basins present both: high rates of taxonomic turnover (as a consequence of high freshwater heterogeneity), and high rates of functional nestedness (considering that primary ray-fined fishes is a close related group we then expect to observe a functional traits convergence pattern) (Albert & Reis, 2011; Cianciaruso, Silva & Batalha, 2009; Logez, Pont & Ferreira, 2010). We further assess if deterministic or stochastic processes are responsible for shaping the observed TβD patterns. Finally, we test the correlation between TβD and FβD.

Methods

Data compilation and study area

We compiled data related to the distribution and functional traits primarily from FishBase (Froese & Pauly, 2017) and complemented this database using checklists, scientific journals, reports, books and collections from museums and universities presented in an online database (see Appendix S1 in Supporting Information). Errors in species names were corrected following Eschmeyer, Fricke and van der Laan (2016), when species was not registered in FishBase. We excluded geo-referenced data from the following cases: (1) non-confirmed species (genus followed by aff., sp., cf.), (2) species with wrong coordinates, and (3) exotic species kept in aquariums (not collected from Brazilian rivers).

We used three spatial scales in our analysis. They include the first and the second classification levels of *Otto Pfafstetter* basins (hereafter called Otto1 and Otto2; (ANA, 2017)) and all Brazilian states (Fig. 1: A – Otto1; B – Otto2; and C – states). We included the state division in our analyses because of the relevance of this division to management policy (Barletta *et al.*, 2016). For instance, national bulletins report catch statistics by state, taking into account how each state has been exploiting its freshwater fish stocks. Furthermore, conservation units in Brazil are divided into federal and state jurisdictions (Gurgel *et al.*, 2009).

For occurrence in Brazilian states, data were directly uploaded to the central database of FishBase hosted in Philippines using remote data entry (RDE). The *Pfafstetter* drainage basin classification have been broadly used to classify freshwater environments for research and management purposes, e.g. "*Agência Nacional das*

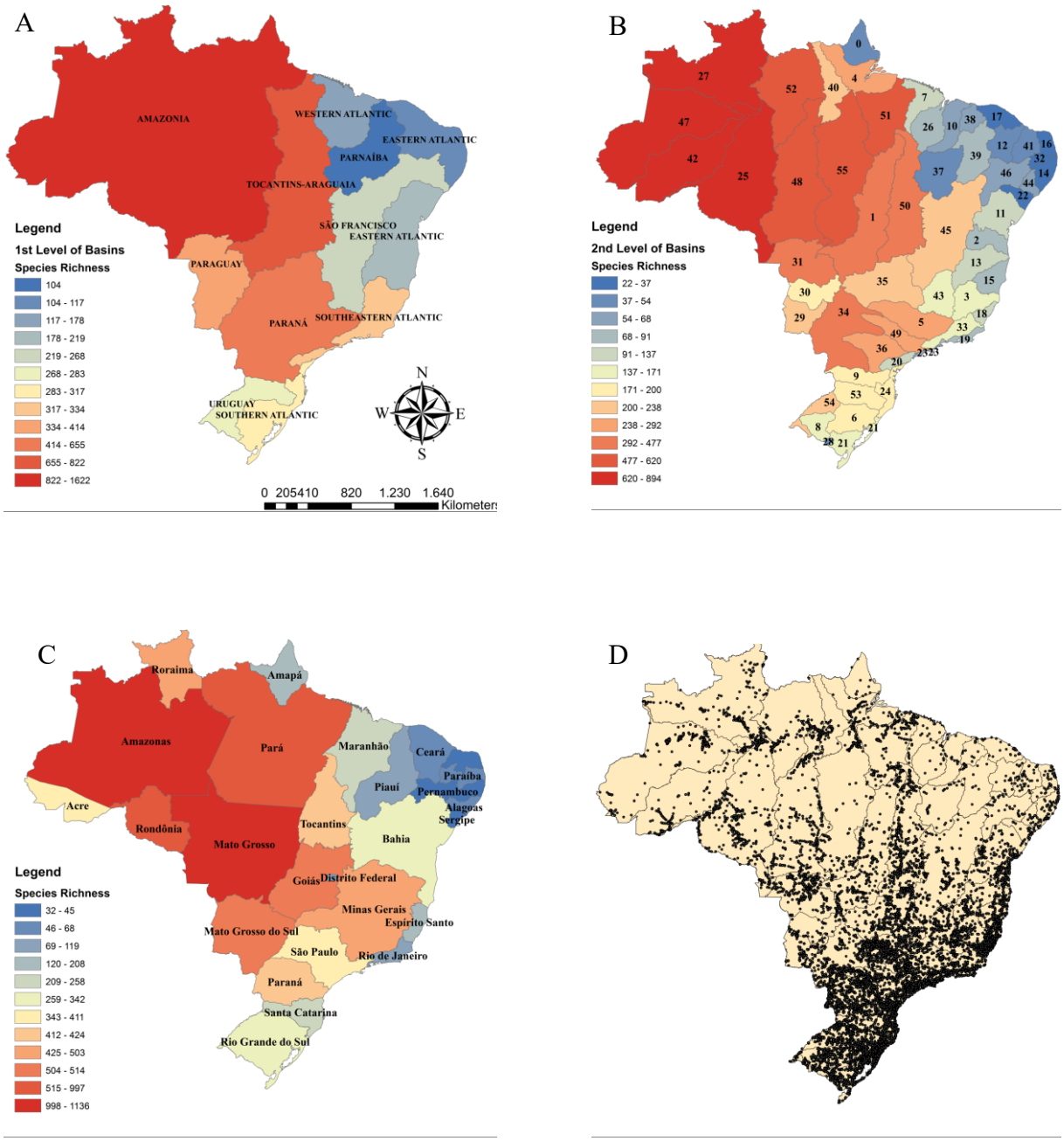


Figure 1 Spatial scales used: A - Otto1 basins (12 units) and its species richness per basin. B** - Otto2 basins (56 units) and its species richness. C - Brazilian states and its species richness. D - Otto2 basins filled with all geo-referenced occurrence points compiled. **Otto2 labels: 0 Amapá coast, 1 Araguaia, 2 Contas, 3 Doce, 4 Amazonas mounth, 5 Grande, 6 Guaíba, 7 Gurupi, 8 Ibicuí, 9 Iguaçu, 10 Itapecuru, 11 Itapecuru-Paraguaçu, 12 Jaguaribe, 13 Jequitinhonha, 14 al PE PB coast, 15 BA ES coast, 16 CE PB coast, 17 CE PI coast, 18 ES coast, 19 RJ coast, 20 RJ SP coast, 21 RS coast, 22 SE coast, 23 SP coast, 24 SP PR SC coast, 25 Madeira, 26 Mearim, 27 Negro, 28 Negro RS, 29 Paraguay 01, 30 Paraguay 02, 31 Paraguay 03, 32 Paraíba, 33 Southern Paraíba, 34 Paraná rh1, 35 Paranaíba, 36 Paranapanema, 37 High Parnaíba, 38 Lower Parnaíba, 39 Medium Parnaíba, 40 Paru, 41 Piranhas, 42 Purus, 43 High São Francisco, 44 Lower São Francisco, 45 Medium São Francisco, 46 Sub-Medium São Francisco, 47 Solimões, 48 Tapajós, 49 Tietê, 50 High Tocantins, 51 Lower Tocantins, 52 Trombetas, 53 High Uruguay, 54 Medium Uruguay, 55 Xingu.

Águas - ANA*"* in Brazil (National Agency of Waters) and by the International Union for Conservation of Nature – IUCN (ANA, 2017; IUCN, 2016). All data were classified into Otto1 and Otto2 using the geographical coordinates of streams, rivers and basins presented on the sources used or estimated using their names along with any other locality information. We classified the species compiled into: primary (species strictly confined to fresh water), secondary (freshwater species that occasionally enter the sea for short periods), and peripheral species (freshwater species very tolerant to saltwater) according to Myers (1949) and Froese and Pauly (2017). We used only species classified as primary ray-finned fishes to build three different assemblage matrices (Otto1, Otto2 and states).

Taxonomic beta diversity

Indices of taxonomic dissimilarity among basins were estimated using incidence matrices built for each spatial scale. Firstly, we partitioned the total dissimilarity across all watersheds using the Jaccard index to separate the total contribution of the turnover and nestedness components of β-div using the *betapart* package (Baselga & Orme, 2012). We constructed dissimilarity matrices between each pair of basins for Otto1 and Otto2 basins, and between pairs of states in order to compare the variation in TβD and FβD among the three scales used. We created a null model to assess how the observed composition of the ichthyofauna differs from a composition obtained from a 999-times randomization procedure and then we calculated the chance of finding dissimilarities values higher than the observed (which here stands as p-value).

Functional beta diversity

Measures of functional diversity depends on the number and type of traits available (Petchey & Gaston, 2002; Swenson, 2014). To estimate FβD, we obtained all biological and ecological trait data available in FishBase, and selected those traits with more availability for the species compiled. We ended with five continuous and two categorical traits for the analysis. Continuous traits were (1) the standard length (SL in cm), (2) food consumption per unit of biomass (Q/B), (3) length at first maturity (L_m in cm), (4) trophic level, (5) the slope of the length-weight relationship. Categorical traits included (6) resilience (capacity of withstanding natural and anthropogenic

disturbances); and (7) position in water column (Table 1). These functional traits describe the functional space occupied by each species, considering the position of species in the trophic web, how well species convert food into biomass, reproduction strategy (here represented by the length at first maturity), the capacity that species has to stand for exploitation or disturbances, and the position of fish in the water column (Table 1).

Although these traits were available for most species, there were gaps of some traits for some species. To overcome these gaps in the functional matrix, we performed an imputation approach based on random forest algorithms. The approach deals with nonparametric missing value (categorical and continuous data) imputation. According to Penone *et al.* (2014), the algorithm: "Train a random forest on observed values, predict the missing values using other variables and trained random forest, then proceed iteratively". This step was done with the R package *missForest* (Stekhoven & Bühlmann, 2012).

In order to estimate the functional hyperspace of each species, we build a distance matrix between species according their traits using the Gower distance, which is appropriate for mixed (e.g., continuous and categorical) data and then obtained the species trait-space through a principal coordinate analysis - PCoA. To partition the turnover and nestedness components from the FβD, we used the framework proposed by Villéger, Grenouillet and Brosse (2013). This approach is based on a multidimensional functional space, in which the convex hull volume describes the functional space that a given community occupy (Villéger, Mason & Mouillot, 2008). This framework required the community matrix for each scale analyzed (one for each spatial level) and the coordinate matrix with functional distances obtained from the PCoA. We tested the efficiency of the functional space by the mean square deviation (mSD) of Euclidean Distance, in which lower mSD represents higher quality in functional space (Maire *et al.* (2015). To test the correlation between TβD and FβD and between their components, we used Mantel permutational test (Legendre & Legendre, 2012). Functional richness for each spatial scale was calculated as the volume of multidimensional space occupied by all species in a community, using the function *multidimFD* (Mouillot *et al.* (2013). All analyses were performed using the R environment (R Core Team, 2016).

Table 1 Functional traits selected to estimate the FβD and functional diversity indices (functional richness).

Traits	Gap (%)	Biological meaning
Maximum Length*	16	Standard length (SL) in cm, when values given were total length (TL) we transformed the values into SL. Size is a functional attribute that is related to metabolism, trophic impacts, nutrient cycling and locomotion.
(Q/B)*	12	Food consumption per unit biomass represents how well a species or population transform food into biomass (Pauly 1986).
Lm*	11	Mean length at first maturity, i.e., the mean length at which juvenile fish become sexually mature for the first time. This is one of the most important traits for fisheries management and reflects the size in which each species start to breed (Froese and Pauly 2016).
Trophic Level*	2	Expresses where fishes tend to operate in their respective food webs (Christensen and Pauly 1993).
b (LWR)*	3	Length-weight relationships ($W = aL^b$) are important in fisheries science, notably to raise length-frequency samples to total catch, or to estimate biomass from underwater length observations ($2.5 < b < 3.5$). Negative allometric: $b<3$ (indicates a decrease in condition or elongation in form with increase in length), isometric: $b=3$, positive allometric: $b<3$ (increase in relative body thickness or plumpness, indicates an increase in condition or increase in height or width with increase in length) (Froese 2006).
Resilience**	53	Capacity of a system to tolerate impacts without irreversible change in its outputs or structure. Often understood as the capacity to withstand exploitation (Froese and Pauly 2016). (Very low, low, medium and high)
Position in water column**	2	Position of fish in the water column (Froese and Pauly 2016). (demersal, bento pelagic, pelagic and pelagic-neritic).

*Continuous traits, **Categorical traits, Gap (%): percentage of NA's (not avaiable).

Results

Taxonomic beta diversity

The entire dataset encompassed 142,405 occurrence records of 2745 primary ray-finned fishes (7 orders and 42 families), of which 95% were from SpeciesLink database and the remaining from other sources (Appendix S1). Most species belonged to two main orders, Siluriformes (49% of all species) and Characiformes (45%), within which Characidae (673 species) and Loricariidae (586) were the most speciose families (Table 2). The 12 basins from Otto1 varied in species richness from 104 to 1622 (mean = 444 ± 409 sd), with Amazon basin having the highest (1622) species richness (Fig. 1 A). The 56 basins from Otto2 ranged from 22 to 894 species (mean = 224 ± 212 sd), with Madeira basin having the highest richness (894 species) (Fig. 1 B, see basin number 25). Mato Grosso (1136) and Amazonas (1074) were the states with the greatest primary ray-finned fish richness (Fig. 1 C). Brazilian 27 states fish richness varied from 22 to 1136 (mean = 351 ± 307 sd). The geo-referenced occurrence records were clustered mainly at Southern and South-eastern regions (Fig. 1 D).

Table 2 Number of primary ray-finned fishes (2745 species) by Order and Family from Brazil.

ORDER		**ORDER**		**ORDER**	
FAMILY	No	FAMILY	No	FAMILY	No
Siluriformes	**1339**	**Characiformes**	**1223**	**Gymnotiformes**	**161**
Loricariidae	586	Characidae	673	Apteronotidae	62
Trichomycteridae	148	Anostomidae	120	Sternopygidae	31
Callichthyidae	147	Curimatidae	84	Gymnotidae	28
Heptapteridae	117	Serrasalmidae	71	Hypopomidae	25
Pimelodidae	94	Crenuchidae	69	Rhamphichthyidae	15
Auchenipteridae	90	Lebiasinidae	41	**Cypriniformes**	**12**
Doradidae	81	Hemiodontidae	29	Cyprinidae	12
Aspredinidae	24	Iguanodectidae	25	**Perciformes**	**6**
Pseudopimelodidae	24	Bryconidae	20	Centrarchidae	2
Cetopsidae	21	Triportheidae	19	Osphronemidae	2
Scoloplacidae	5	Parodontidae	18	Polycentridae	2
Clariidae	1	Erythrinidae	13	**Osteoglossiformes**	**3**
Ictaluridae	1	Prochilodontidae	13	Osteoglossidae	2
		Chilodontidae	8	Arapaimidae	1
		Gasteropelecidae	8	**Acipenseriformes**	**1**
		Cynodontidae	7	Polyodontidae	1
		Ctenoluciidae	5		

Regarding the contribution of turnover and nestedness components of TβD at the different scales, turnover contributed with 93% for Otto1 (Jaccard Dissimilarity Index: 0.953), 98% for Otto2 (0.983) and 95% for Brazilian states (0.967) (Table 3). The three scales showed that the high level of TβD, measured by the Jaccard Dissimilarity Index (from 0; communities sharing the same species, to 1; communities without any common species), was due to high levels of turnover (Fig. 2). For example, 28% of all species occurred only in one basin from the Otto2 scale, whereas 15 species occurred in more than 30 different basins, the largest distributed species were: *Hoplias malabaricus* (54 Otto2 basins), *Astyanax bimaculatus* (53 basins), *Callichthys callichthys* (44), *Gymnotus carapo* (44), *Rhamdia quelen* (43), (Fig. 3). The pattern of TβD among basins was significantly higher than that expected by chance ($p<0.001$) (Table 3).

Table 3 Components of the TβD (Jaccard index) observed and comparison between the mean samples and standard deviation for primary ray-finned fishes in Brazil.

Otto1	TβD *	mean.samples**	sd**	sig.code	%β-div
beta.JAC	0.953	0.939	0.009	0***	
beta.JNE	0.066	0.080	0.024	0***	7
beta.JTU	0.886	0.858	0.025	0***	93
Otto2					
beta.JAC	0.983	0.884	0.028	0***	
beta.JNE	0.023	0.064	0.022	0***	2
beta.JTU	0.961	0.949	0.009	0***	98
States					
beta.JAC	0.967	0.939	0.009	0***	
beta.JNE	0.045	0.079	0.026	0***	5
beta.JTU	0.922	0.860	0.029	0***	95

*TβD observed, estimated using the data.multi function from betapart package. ** The mean of randomized TβD values found with the beta.sample function (samples=999). *** ANOVA level of significance ($p<0.001$). JAC: Jaccard Dissimilarity Index, JTU: turnover component of JAC, JNE: nestedness component of JAC. %β-div: proportional turnover and nestedness contributions to beta diversity.

Functional beta diversity

The first four PCoA axes had a mean square deviation (mSD) of 0.0040 (for 2 Dimensions), 0.0023 (3D) and 0.0022 (4D) (Fig. 4), thus we selected only the first three axes to optimize the best computation time due to the high number of species used for each level (Otto1 and Otto2 basins, and states). FβD was highly defined by nestedness, contrasting the results found for TβD in all scenarios. Otto1 basins had a mean FβD of 0.325 which represents a nestedness contribution of 70%, whereas Otto2 basins showed a mean FβD of 0.442 with a nestedness contribution of 80%. For Brazilian states, the nestedness contribution was 84% of total FβD 0.410 (Table 4).

Table 4 Statistical summary of FβD (Jaccard index) for primary ray-finned fishes in Brazil using three scales of observation.

Otto1	FβD*	sd.	%β-div
beta.JAC	0.325	0.104	
beta.JNE	0.227	0.156	70
beta.JTU	0.098	0.105	30
Otto2			
beta.JAC	0.442	0.173	
beta.JNE	0.355	0.226	80
beta.JTU	0.087	0.104	20
States			
beta.JAC	0.410	0.184	
beta.JNE	0.346	0.228	84
beta.JTU	0.065	0.085	16

* FβD observed, estimated using the function multidimFbetaD (Villegér etal., 2013). JAC: Jaccard Dissimilarity Index, JTU: turnover component of JAC, JNE: nestedness component of JAC. %β-div: proportional turnover and nestedness contributions to beta diversity.

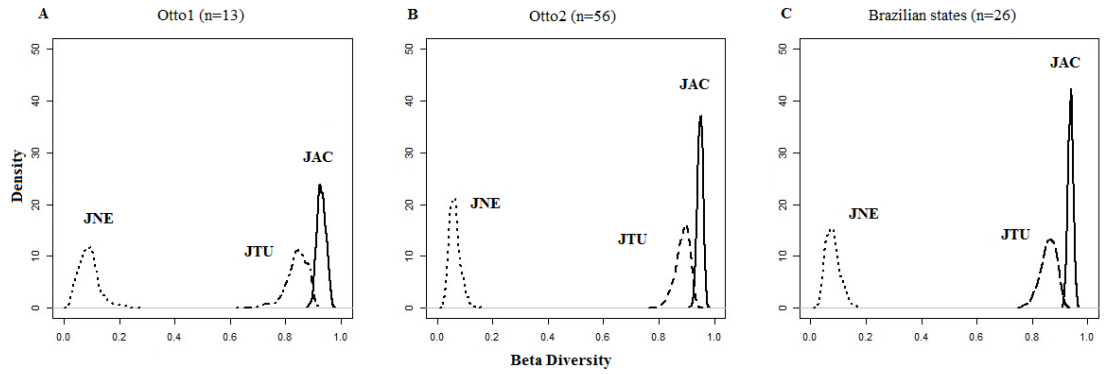


Figure 2 Total dissimilarities represented by Kernel density (y axis) and TβD (x axis) of Otto Pfafstetter level 1 and 2 basins: A - Otto1, B - Otto2, and C - Brazilian states. JAC – Jaccard dissimilarity (total β-div). JTU – (turnover component of Jaccard dissimilarity). JNE – Nestedness component of Jaccard dissimilarity.

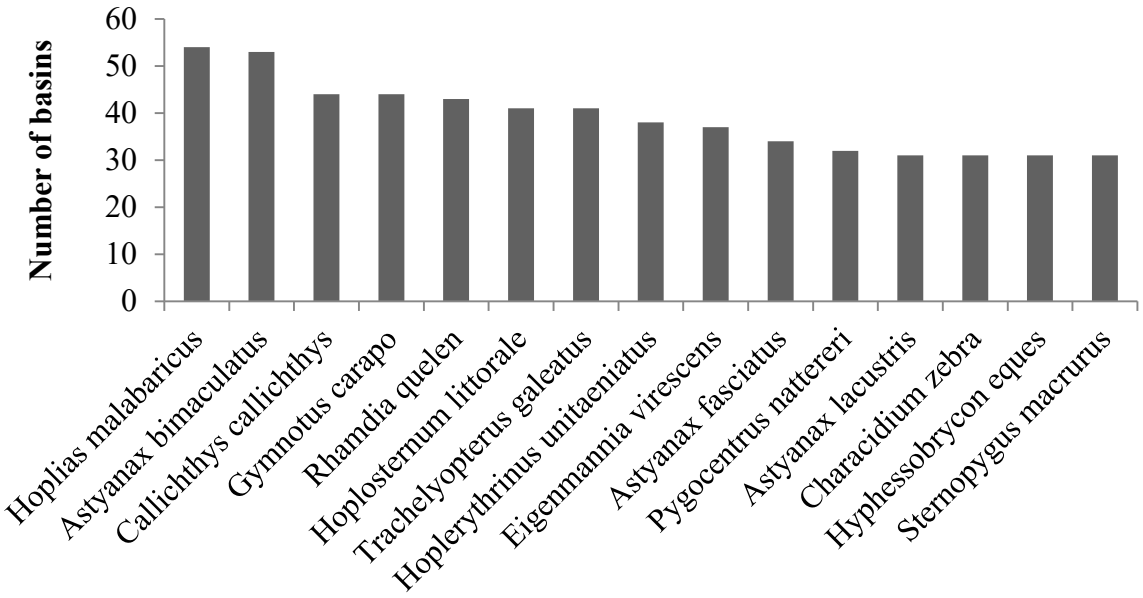


Figure 3 Occurrence range (by number of Otto2 basins) of the most widely distributed primary ray-finned fish species from Brazil.

The volume's percentage of the functional space occupied by each basin, which here we express as the functional richness, varied between 38% (Western Atlantic) to 91% (Amazonia) for Otto1 basins (Fig. 5, A and B), and between 14% (CE PI coast; basin 17) to 88% (Madeira, basin 25) for Otto2 basins (Fig. 5, C and D). The states functional richness ranged from 21% (Ceará) to 91% (Mato Grosso). Mantel tests based on randomizations showed significant correlations between taxonomic TβD and FβD, as long with its respective components at all scales ($p<0.001$) (Fig. 6).

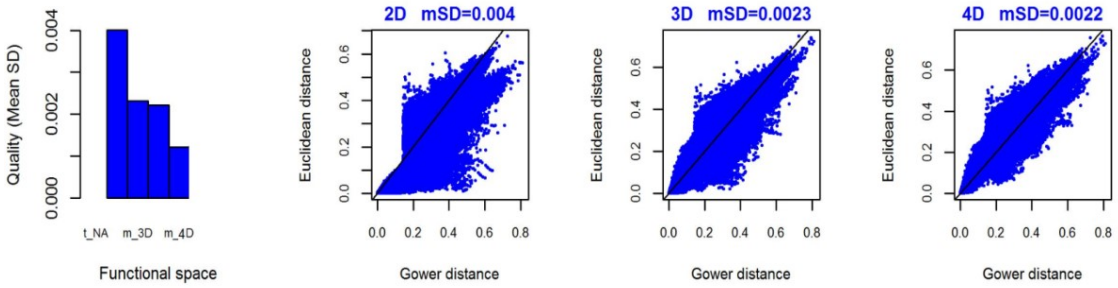


Figure 4 Quality of the functional space measured by the mean square root (mSD) from four coordinates axes built using principal coordinates analysis - PCoA. The best quality is represented by the lowest mSD (Maire *et al.*, 2015).

Discussion

We have shown that primary ray-finned fishes from Neotropical region presented high rates of taxonomic turnover for all scales (Figure 2). This pattern is associated with regions that experienced a process of Quaternary climate stability, which can favor persistence and also speciation of the species pool (Leprieur *et al.*, 2011). Other key factors that influence high rates of taxonomic turnover in this region are the high freshwater heterogeneity (Guégan, Lek & Oberdorff, 1998; Heino, 2011), lower dispersal ability of fishes and the complex hydrology and geomorphology history formation in the region (Albert & Reis, 2011). In addition, contrary to the low rates of taxonomic nestedness (Table 3), we found a trend of high functional nestedness (Table 4). This result shows that the high replacements of primary ray-finned fishes between basins occur with species that present similar functional traits values (functionally redundant species). High functional nestedness in primary ray-finned fishes is associated with allopatric speciation (Albert & Reis, 2011), or functional convergence (Logez, Pont & Ferreira, 2010), since the primary ray-finned fishes are considered as a close related group (Nelson, Grande & Wilson, 2016). Lastly, our analysis revealed a high correlation between total TβD and FβD (Fig. 6).

After showing that the observed TβD was significantly greater than that expected at random (Table 3), we can conclude that deterministic processes, which may include niche-based process (e.g., environmental filtering and biotic interactions) play a more important role as an ecological process shaping the patterns of composition of primary ray-fined fish at Neotropics than stochastic processes do. Comparing the results

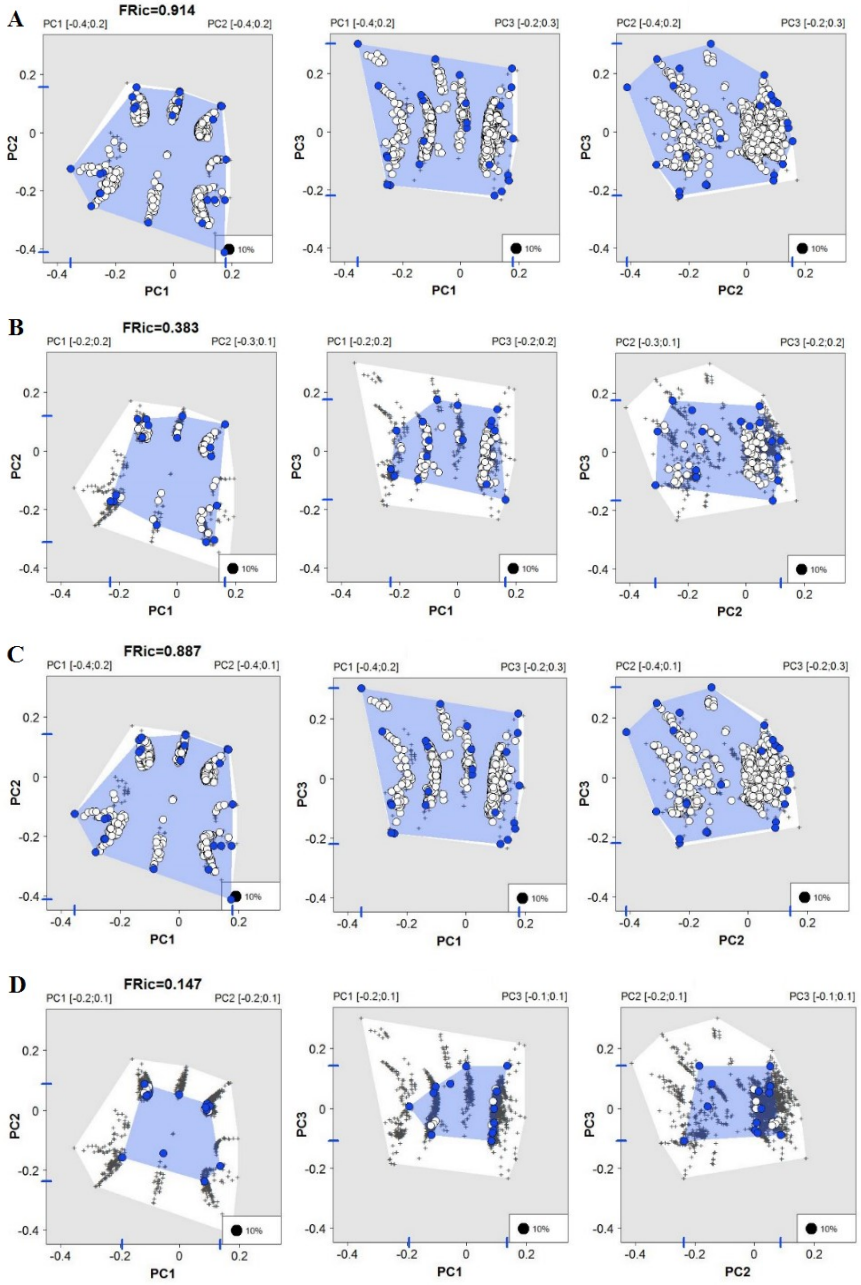


Figure 5 Representation of three Principal Coordinate Analysis axes of multidimensional functional richness indices for A -Amazonia basin, B - Western Atlantic, C - Madeira and D - CE PI Coast. Otto1: A and B, Otto2: C and D. The white shapes represents 100% of the functional spaces occupied by all species presented in all basins and the blue shape represents the amount of functional spaces that the fish traits of each basin occupy. FRic: (proportion of functional space filled by species present in the assemblage). Minimum and maximum values on each axis are illustrated by small blue bars. White and blue symbols are species being vertices in the multidimensional space.

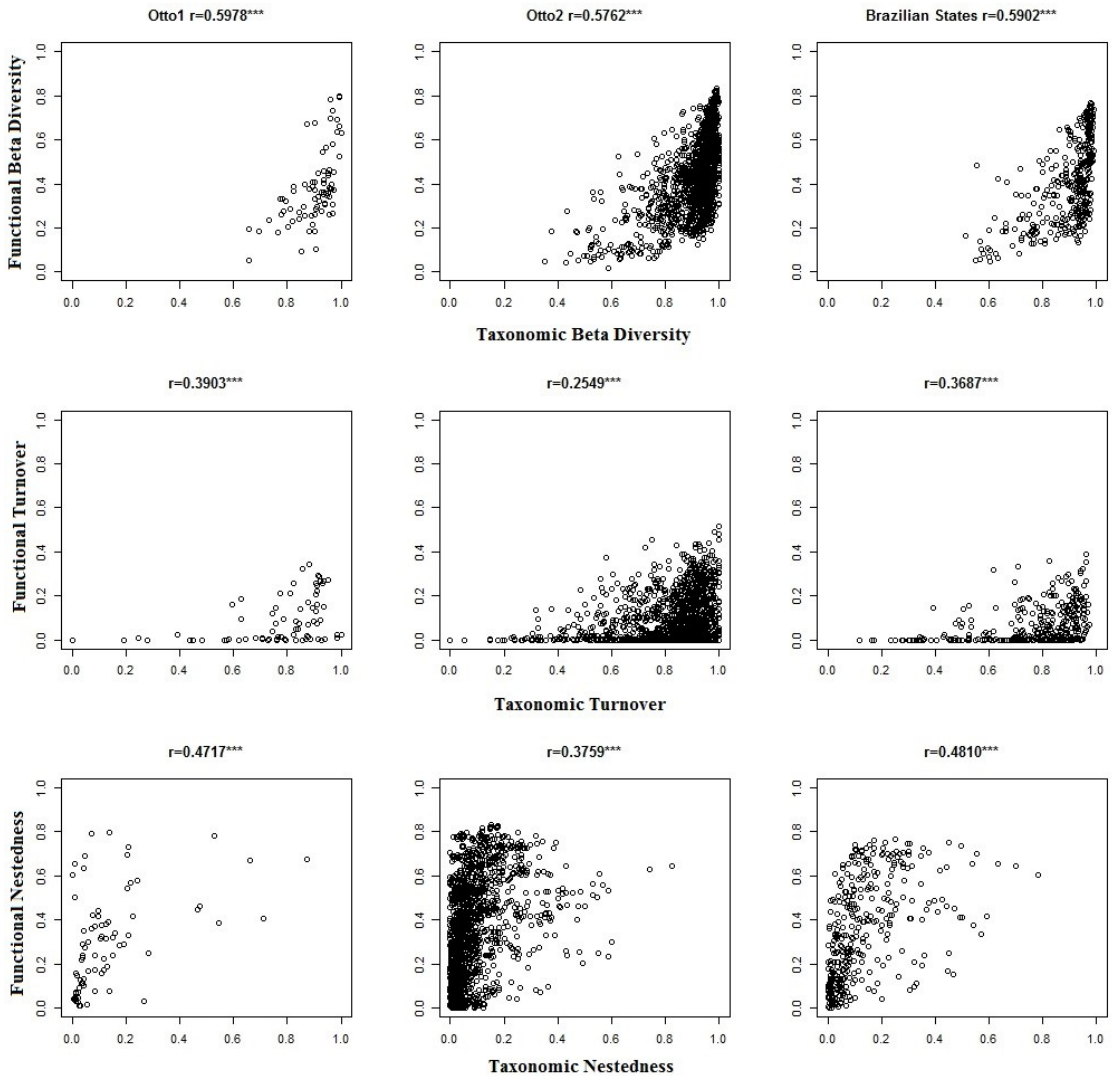


Figure 6 Correlation between total TβD and FβD (first row); taxonomic and functional turnover (second row); taxonomic and functional estedness (third row) for three spatial scales: Otto1 (first column), Otto2 (second column) and Brazilian States (third column). (r: Pearson) *** Correlation coefficient indicates significant results for Mantel test ($p<0.001$).

found for Otto1, Otto2 we noticed that the TβD and FβD were higher for Otto2 (smaller basins) (Table 3 and 4). These results highlight the fact that the species compositions differ highly, even in a smaller scale, indicating strong isolation between communities.

We provide evidence of the influence of scale on β-div, as also pointed by Hepp and Melo (2013) for a Neotropical Region. Two main mechanisms or paradigms have been proposed to explain the metacommunity structure (consequently for β-div) in freshwater environments: (i) the species-sorting paradigm, by which environmental variations are correlated with species distribution; (ii) mass-effects paradigms, which

poses that niche-based processes and dispersal ability are relevant in the shaping process of the structure of different communities (Melo *et al.*, 2011; Leibold *et al.*, 2004). Hence, one can expect contrasting contributions of turnover and nestedness for TβD in different regions and scales of observation.

Correlations between distinct aspects of biodiversity (TβD and FβD) suggest that one can use taxonomic or functional diversity as a surrogate of each other. However, the use of taxonomic diversity as a surrogate for functional diversity requires caution (Carvalho & Tejerina-Garro, 2015). It is needed to consider the specific locality (complexity, heterogeneity, abiotic and biotic parameters). The community of primary ray-finned fishes from Amazonia Otto1 and Madeira Otto2 basins occupied most of the functional space from all Brazilian basins (Figure 6). Assessing the functional richness of different communities shows various life history strategies within a region. Functional diversity is of great relevance to understand the contribution of each community to ecosystem functioning (Mouchet *et al.*, 2010; Mason *et al.*, 2005). A global assessment of fish functional richness between 6 biogeographic regions (Afrotropical, Australian, Neartic, Neotropical, Oriental and Paleartic), presented lower functional turnover (0.324 ± 0.206), while the taxonomic turnover between species of those realms was (0.982 ± 0.022) (Toussaint *et al.*, 2016). That global assessment (considering each realm as α-div and the γ-div as the entire globe) also attributed the nesting pattern in functional diversity of freshwater fishes as a process of biological traits been shared between realms.

Regarding the role of the state divisions for natural resources management, we found that the contribution of turnover and nestedness for TβD and FβD at the state level followed the same patterns of Otto1 and Otto2 basins (Figure 2). Mato Grosso and Amazonas are the states with most taxonomic and functional richness, its territory encompasses the most functionally representative basins from Brazil (Fig. 1 B: Madeira; 25, Tapajós; 48, Solimões; 47 and Negro; 27). This study presented an updated list of species by state (Appendix S1). Continental fisheries management (based on ecosystem approaches to fisheries) integrates many ecological aspects (such as taxonomic and functional diversities) (Fischer *et al.*, 2015), in order to develop better management strategies. The basic information for fisheries management and stock assessment are the number of species per area (for continental fisheries: basins or states) and functional traits (Hilborn & Walters, 1992).

We demonstrated that the usage of TβD and FβD approaches, at different spatial scales, can be a useful tool to understand how species composition and functional traits change from place to place (McKnight *et al.*, 2007; Villéger, Grenouillet & Brosse, 2014). Turnover patterns across space and time are also able to give specific clues regarding how ecosystems change (Magurran, 2016). Conservation biologists and stakeholders can take measures regarding conservation efforts knowing the dynamic nature of β-div at any biodiversity facet (taxonomic, functional or phylogenetic diversity), monitoring how the variations between communities respond to disturbances. Increasing or decreasing β-div will depend if new species are been introduced in a new environment or been extirpated from its natural habitat (Socolar *et al.*, 2016).

Knowledge deficits still plague investigation of biodiversity patterns in the Tropics. Our geo-referenced dataset showed that the number of occurrence data was more clustered in southern and southeastern regions than in northern and northeastern regions (Figure 1 D). Furthermore, a scientometric analysis of articles on freshwater fisheries demonstrated a tendency of disregarding scientific knowledge when dealing with freshwater fisheries, which leads to a poor decision making process of management for these resources (Alves & Minte-Vera, 2013). According to that study, the lowest number of studies was carried on in the northeastern region. Freshwater fisheries management in developing countries is poorly invested. 'Integrated research and management', is pointed as an important step with the objective of improving conservation strategies in South America (Olden *et al.*, 2010; Barletta *et al.*, 2016).

Freshwater habitat loss is a well-recognized issue in South America (Costa & Barletta, 2016). Only 16.7% of the continental and 1.4% of the marine territory in Brazil is protected (IPEA, 2009) and it is urgent to extend this percentage to cover less protected areas. Conservation strategy can be better designed if we can predict how disturbing actions could drive the changes in the different aspects of biodiversity, i.e. community homogenization caused by potential fish invasions (Villéger, Grenouillet & Brosse, 2014) or habitat lost (Costa & Barletta, 2016). In this study we also presented the most updated list of species (α-div) for all Brazilian hydrological basins based on the *Otto Pfafstetter* classification. This is the most basic information required to develop large-scale ichthyological conservation schemes for these basins and promote the proper management of their stocks, ensuring the food security of many riverine communities (McIntyre, Liermann & Revenga, 2016).

Conclusions

In this study we shed more light on the comprehension of how the taxonomic and functional biodiversity of primary ray-finned fishes (Actinopterygii fishes restricted to freshwater environments) from Neotropics (using Brazil as the most representative country within the region) is structured. Using the beta diversity approach, e.g. measure of variations between communities for the taxonomic and functional facets of biodiversity, showed that the patterns of taxonomic beta diversity in three scales of observation (two levels of hydrological basins and Brazilian states) were ruled by high contribution of turnover (replacement of species among communities). Conversely, the patterns of functional beta diversity had high contribution of nestedness (communities sharing the same functional space volume). Thus, the functional diversity is driven by functionally redundant species in the Neotropical Region, even in a scenario of high replacement of species between basins. Therefore, we have shown that taxonomic structure is affected by deterministic, niche-based processes, such as environmental filtering and biotic interactions. The only way to maintain the gamma diversity (the species pool of certain region) is to comprehend how modifications or disturbances in the level of alpha diversity (local diversity) affect higher spatial levels.

References (Freshwater Biology formating)

Albert J.S. & Reis R.E. (2011) *Historical biogeography of Neotropical freshwater fishes,* Univ of California Press.

Alves D.C. & Minte-Vera C.V. (2013) Scientometric analysis of freshwater fisheries in Brazil: repeating past errors? *Reviews in Fish Biology and Fisheries,* **23,** 113-126.

Ana. (2017) Agência Nacional das Águas. Ministério do Meio Ambiente. Divisão Hidrográfica: metadados. Vol. 05 Jan.

Barletta M., Cussac V.E., Agostinho A.A., Baigún C., Okada E.K., Catella A.C., Fontoura N.F., Pompeu P.S., Jiménez-Segura L.F. & Batista V.S. (2016) Fisheries ecology in South American river basins. *Freshwater Fisheries Ecology***,** 311-348.

Baselga A. & Orme C.D.L. (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution,* **3,** 808-812.

Cardoso P., Rigal F., Carvalho J.C., Fortelius M., Borges P.A., Podani J. & Schmera D. (2014) Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. *Journal of Biogeography,* **41,** 749-761.

Carvalho R.A. & Tejerina-Garro F.L. (2015) Relationships between taxonomic and functional components of diversity: implications for conservation of tropical freshwater fishes. *Freshwater Biology,* **60,** 1854-1862.

Chase J.M. & Myers J.A. (2011) Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* **366,** 2351-2363.

Cianciaruso M.V., Silva I.A. & Batalha M.A. (2009) Diversidades filogenética e funcional: novas abordagens para a Ecologia de comunidades. *Biota Neotropica,* **9,** 93-103.

Costa M. & Barletta M. (2016) Special challenges in the conservation of fishes and aquatic environments of South America. *Journal of Fish Biology*.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.-I., Knowler D.J., Lévêque C., Naiman R.J., Prieur-Richard A.-H., Soto D. & Stiassny M.L. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews,* **81,** 163-182.

Eschmeyer W.N., Fricke R. & Van Der Laan R. (2016) Catalog of fishes: genera, species, references. Vol. December.

Fischer J., Jorgensen J., Josupeit H., Kalikoski D.C. & Lucas C.M. (2015) *Fishers' Knowledge and the Ecosystem Approach to Fisheries: Applications, Experiences and Lessons in Latin America*.

Froese R. & Pauly D. (2017) FishBase. Vol. January.

Guégan J.-F., Lek S. & Oberdorff T. (1998) Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature,* **391,** 382-384.

Gurgel H.C., Hargrave J., França F., Holmes R.M., Ricarte F.M., Dias B.F., Rodrigues C.G. & Brito M.C.W.D. (2009) Unidades de conservação e o falso dilema entre conservação e desenvolvimento.

Heino J. (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology,* **56,** 1703-1722.

Hepp L.U. & Melo A.S. (2013) Dissimilarity of stream insect assemblages: effects of multiple scales and spatial distances. *Hydrobiologia,* **703,** 239-246.

Hilborn R. & Walters C.J. (1992) *Quantitative fisheries stock assessment: choice, dynamics, and uncertainty,* Chapman and Hall, New York.

Hubbell S.P. (2001) *The unified neutral theory of biodiversity and biogeography (MPB-32),* Princeton University Press.

Ipea. (2009) Instituto de Pesquisa Econômica e Aplicada. Unidades de conservação e o falso dilema entre conservação e desenvolvimento. Boletim regional, urbano e ambiental. 03 Dez. 2009. 14.

Iucn. (2016) The IUCN Red List of Threatened Species. Version 2016-3. Vol. 07 December.

Koleff P., Gaston K.J. & Lennon J.J. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology,* **72,** 367-382.

Legendre P. & Legendre L.F. (2012) *Numerical ecology,* Elsevier.

Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F., Holt R.D., Shurin J.B., Law R. & Tilman D. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters,* **7,** 601-613.

Leprieur F., Tedesco P.A., Hugueny B., Beauchard O., Dürr H.H., Brosse S. & Oberdorff T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology letters,* **14,** 325-334.

Logez M., Pont D. & Ferreira M.T. (2010) Do Iberian and European fish faunas exhibit convergent functional structure along environmental gradients? *Journal of the North American Benthological Society,* **29,** 1310-1323.

Magurran A.E. (2016) How ecosystems change. *Science,* **351,** 448-449.

Maire E., Grenouillet G., Brosse S. & Villéger S. (2015) How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Global Ecology and Biogeography,* **24,** 728-740.

Mason N.W., Mouillot D., Lee W.G. & Wilson J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos,* **111,** 112-118.

Mcintyre P.B., Liermann C.a.R. & Revenga C. (2016) Linking freshwater fishery management to global food security and biodiversity conservation. *Proceedings of the National Academy of Sciences***,** 201521540.

Mcknight M.W., White P.S., Mcdonald R.I., Lamoreux J.F., Sechrest W., Ridgely R.S. & Stuart S.N. (2007) Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS Biol,* **5,** e272.

Melo A.S., Schneck F., Hepp L.U., Simões N.R., Siqueira T. & Bini L.M. (2011) Focusing on variation: methods and applications of the concept of beta diversity in aquatic ecosystems. *Acta Limnologica Brasiliensia,* **23,** 318-331.

Mouchet M.A., Villeger S., Mason N.W. & Mouillot D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology,* **24,** 867-876.

Mouillot D., Albouy C., Guilhaumon F., Lasram F.B.R., Coll M., Devictor V., Meynard C.N., Pauly D., Tomasini J.A. & Troussellier M. (2011) Protected and threatened components of fish biodiversity in the Mediterranean Sea. *Current Biology,* **21,** 1044-1050.

Mouillot D., Graham N.A., Villéger S., Mason N.W. & Bellwood D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in ecology & evolution,* **28,** 167-177.

Myers G.S. (1949) Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems. *Bijdragen tot de Dierkunde,* **28,** 315-322.

Nelson J.S., Grande T.C. & Wilson M.V. (2016) *Fishes of the World,* John Wiley & Sons.

Olden J.D., Kennard M.J., Leprieur F., Tedesco P.A., Winemiller K.O. & García-Berthou E. (2010) Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and Distributions,* **16,** 496-513.

Pelayo-Villamil P., Guisande C., Vari R.P., Manjarrés-Hernández A., García-Roselló E., González-Dacosta J., Heine J., González Vilas L., Patti B. & Quinci E.M. (2015) Global diversity patterns of freshwater fishes–potential victims of their own success. *Diversity and Distributions,* **21,** 345-356.

Penone C., Davidson A.D., Shoemaker K.T., Di Marco M., Rondinini C., Brooks T.M., Young B.E., Graham C.H. & Costa G.C. (2014) Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution,* **5,** 961-970.

Petchey O.L. & Gaston K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology letters,* **5,** 402-411.

Pool T.K., Grenouillet G. & Villéger S. (2014) Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. *Diversity and Distributions,* **20,** 1235-1244.

R Core Team. (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Socolar J.B., Gilroy J.J., Kunin W.E. & Edwards D.P. (2016) How should beta-diversity inform biodiversity conservation? *Trends in ecology & evolution,* **31,** 67-80.

Soininen J., Lennon J.J. & Hillebrand H. (2007) A multivariate analysis of beta diversity across organisms and environments. *Ecology,* **88,** 2830-2838.

Stekhoven D.J. & Bühlmann P. (2012) MissForest—non-parametric missing value imputation for mixed-type data. *Bioinformatics,* **28,** 112-118.

Strayer D.L. & Dudgeon D. (2010) Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society,* **29,** 344-358.

Swenson N.G. (2014) *Functional and phylogenetic ecology in R,* Springer.

Toussaint A., Charpin N., Brosse S. & Villéger S. (2016) Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. *Scientific reports,* **6**.

Tuomisto H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography,* **33,** 2-22.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37,** 130-137.

Villéger S., Grenouillet G. & Brosse S. (2013) Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography,* **22,** 671-681.

Villéger S., Grenouillet G. & Brosse S. (2014) Functional homogenization exceeds taxonomic homogenization among European fish assemblages. *Global Ecology and Biogeography,* **23,** 1450-1460.

Villéger S., Mason N.W. & Mouillot D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology,* **89,** 2290-2301.

Whittaker R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological monographs,* **30,** 279-338.

RESUMO (Artigo 2)

Catastrofes ambientais, quando responsáveis por extinções de espécies locais, podem afetar o compartilhamento de espécies entre comunidades em escalas regionais, a diversidade beta (β-div). Utilizando o 'desastre da barragem de Bento Rodrigues', na Bacia do Rio Doce como um modelo de caso, nós avaliamos as possíveis consequências de diferentes níveis de extinções locais de espécies para a β-div regional e riqueza funcional entre seis bacias vizinhas. Nós avaliamos a amplitude das mudanças na β-div e riqueza funcional usando cinco cenários de extinções, variando entre os padrões antes do desastre até a extirpação total das espécies através de procedimentos randômicos. Uma maior contribuição do nestedness (de 13-19%), levou a um aumento nos padrões de diversidade beta: de 0,75 para 081 (índice de dissimilaridade de Sørensen). A riqueza functional da Bacia do Doce também diminui de 69-36%. Graças ao padrão regional de compartilhamento de espécies entre bacias, as possíveis consequências das extinções de peixes incluem a diminuição na contribuição do turnover (87-81%). O desastre causou mudanças substanciais nos padrões regionais de β-div e riqueza funcional, devido a um processo conhecido como heterogeinização subtrativa. Estes resultados podem ser relevantes para ambos, a conservação local e visão geral de como distúrbios afetam a biodiversidade.

Palavras chave: Desastre de Mariana, turnover, nestedness, diversidade funcional.

Paper a ser submetido na revista Natureza e Conservação (a formatação do artigo 2 segue as normas da revista).

Title

Shifts in taxonomic beta-diversity and functional richness of ray-finned fishes following massive environmental disturbance

Abstract

Environmental catastrophes, when responsible for local species extinctions, can further affect the sharing of species among communities at a regional scale, i.e. the beta-diversity (β-div). Taking the 'Bento Rodrigues dam disaster' at the Doce Basin as a case model, we evaluate the possible consequences of different levels of local species extinctions to the regional taxonomic β-div and functional richness across six neighbour river basins. We assess the range of changes in β-div and functional richness using five scenarios of extinction, ranging from no extinction to total extirpation through randomization procedures. A higher contribution of nestedness from 13-19%, leaded to an increase in the pattern of beta diversity: 0.75 to 0.81 (Sørensen dissimilarity index). The functional richness from Doce Basin also decreased from 69-36%. Owing to the regional pattern of species sharing among basins, the likely consequences of fish extinctions include a decreasing trend of turnover contribution (87-81%). The disaster caused substantial changes on regional patterns of β-div and functional richness, owing to a process known as subtractive heterogenization. These findings might be relevant for both, local conservation purposes and the overview of how disturbance affect biodiversity.

Keywords: Mariana disaster**,** turnover, nestedness, functional diversity

Introduction

Species loss affect multiple facets of biodiversity, including species sharing among communities on regional scale (i.e., beta diversity; β-div hereafter) (Melo *et al.* 2011). However, little is known regarding how species losses alter the components of β-div (Villéger *et al.* 2014). These components represent the differences among communities owing to species replacement (turnover) and discrepancies in local richness (nestedness) (Baselga Andrés 2010). In fact, understanding how species losses from environmental disturbances alter these components may not only be relevant for knowing the regional dynamics of biodiversity, but also to shed light on how ongoing species depletion, due to habitat degradation, may have affected patterns of β-div and its components in a broader sense (Burkhead 2012, Magurran 2016).

The β-div responses facing different scenarios of disturbances are: (i) when shared species disappear from two or more hypothetic communities (subtractive heterogenization), (ii) when some species arrive only in one of two communities (additive heterogenization), both changes leads to an increasing β-div response, (iii) when rare species become extinct from one hypothetic community (subtractive homogenization), (iv) when rare species become more widespread (additive homogenization), both changes leads a decreasing β-div (Dornelas *et al.* 2013, Socolar *et al.* 2016). Conservation biologists and stakeholders can take measures regarding conservation efforts knowing the dynamic nature of β-div at any biodiversity facet (taxonomic, functional or phylogenetic diversity), monitoring or simulating how the variations between communities respond to disturbances (McGill *et al.* 2015).

As species are lost, environmental disturbances also changes the patterns of functional diversity from a given locality or region (Villéger *et al.* 2010). Likewise, disruptions affects one of the primary components of functional diversity, functional richness, known as the amount of the multidimensional space occupied by a set of species from a community within the functional space (Mason *et al.* 2005, Villéger *et al.* 2008). Taxonomic diversity losses could affect the functional richness in different ways, depending on the position of each species into the functional space, e.g. if a given specie that possess extreme combinations of functional traits is eliminated from the environment we expect to observe considerable decrease in the functional space from the community (Mouillot *et al.* 2013). Hence, predicting how different aspects of biodiversity reacts facing anthropocentric or environmental impacts is highly challenging (Dornelas *et al.* 2013).

Although information on which species has been reduced or gone extinct is mandatory, as it would inform precisely the magnitude of the disturbance both locally and regionally, such information may take too long to be assembled. However, anticipating the range of impact of some communities attributes can be recovered quite quickly through a simulation approach. In addition, we can take advantage of pre-disturbance, observed data from a real case of environmental catastrophe to address this question more realistically. The Mariana havoc occurred in November 2015, when an iron mining dam erupted about 50 billion of litters of heavy metal-rich waste at Doce Basin, destroyed villages and collapsed the river ecosystem downstream (Escobar 2015, Fernandes *et al.* 2016). This environmental disaster may have led many species to local extinction or to population depletion that may be hardly recovered. Therefore, it provides a case study to simulate abrupt changes in the regional β-div of freshwater

87 fishes from Doce Basin in relation to the regional species pool, and also to predict possible shifts
88 at the level of functional richness.

89 As the magnitude of the impact is yet unknown we resorted to the available data on the
90 prior fish composition from the Doce Basin and adjacent basins to investigate how the
91 components of the taxonomic β-div (turnover and nestedness) change in amount and direction in
92 response to the disturbance regionally, when different levels of species loss are presumed. We
93 also simulated the possible consequences at the functional richness from Doce Basin in relation
94 to the total functional richness from all its neighbour basins to assess the possible biodiversity
95 losses from Mariana disaster on the sharing of fish species between to affected area and its
96 region.

97 **Material and Methods**

98 **Taxonomic Diversity Shifts**

99 We used the *Otto Pfafstetter* basins classification to delimitate the Doce Basin and six other
100 neighbour basins (Fig. 1). The *Pfafstetter* drainage basins has been broadly used to classify
101 freshwater environments for research and management purposes (ANA 2015, IUCN 2015). We
102 compiled occurrence data of primary ray-finned fish species richness (Actinopterygii fishes
103 restricted to fresh water environments) from each basin from articles, books, check lists and from
104 data available in the online databases specieslink (http://www.splink.org.br/) and FishBase
105 (Froese & Pauly 2017).

106 Dissimilarity indices between basins were estimated using incidence matrices built for
107 each basin. These indices vary from 0 (two communities with the same pool of species) to 1 (two
108 communities with totally dissimilar pool of species). We partitioned the total dissimilarity across

all basins using the Sørensen index to separate the total contribution of the turnover and nestedness components of β-div, following Baselga Andres & Orme (2012). We estimated the β-div for five different scenarios of species loss: with no extinctions and with 25, 50, 75 and 100% of species extinction.

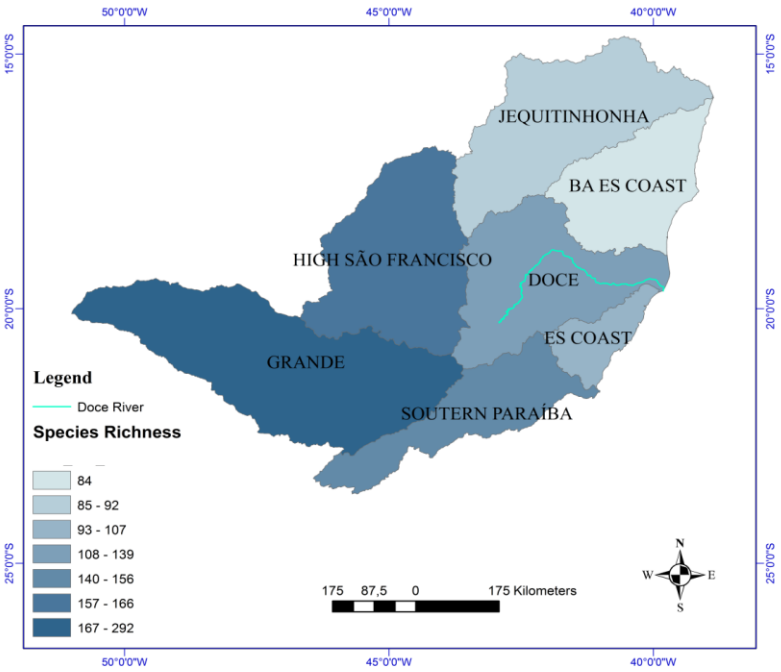


Figure 1. Seven hydrographic basins used in this study showing the Doce River (blue line) and its neighbour basins.

For each extinction level (except for 100%), we allowed the extinction of each proportion of species through a 100 runs randomization procedure. We then estimated the β-div and its components for each run and their average across all randomizations. Analyses were performed in R environment (R Core Team 2016), with the package betapart (Baselga Andres & Orme

2012). We tested differences between scenarios with ANOVA, followed by Tukey test for each β-div component.

Functional Diversity Shifts

For the set of species compiled from all seven basins we used the functional traits available in FishBase (Froese & Pauly 2017). We selected five continuous traits: max size in standard lenghth (cm), the rate of food consumption per unit of biomass (Q/B) (Pauly 1986), length of first maturity (lm in cm), the parameter 'b' from length weight relationship equation, trophic level, and two categorical traits: position in the water column and reproduction strategy, i.e. if species take care of the breed or not (guarders or non-guarders).

We choose the functional traits based on its biological, ecological relevance and the availably of data. Traits were available for most of species compiled, however there were gaps of some traits for some species. In order to fill the gaps (NA's) we used an imputation method in the functional matrix selected, based on random forest algorithms (Penone *et al.* 2014). This approach predicts the missing values using other variables and trained random forest proceeding iteratively. The accuracy of this method have been proven by Pantanowitz & Marwala (2009), then we used the R package *missForest* (Stekhoven & Bühlmann 2012) to complete our functional matrix.

Functional diversity shifts were assessed using two main matrices: (1) Community matrix (presence absence matrix with seven basins, species as rows and basins as columns), and; (2) Functional coordinates matrix (species as rows and each column represent one dimension from the principal coordinate analyses – PCoA) (Villéger *et al.* 2013). The coordinate matrix were built firstly using the Gower's distance with equal weights (respecting categorical and

149 continuous traits) over the original functional matrix (species as rows and traits as columns) then
150 we applied a PCoA over the Gower's matrix distances (Villéger *et al.* 2008).

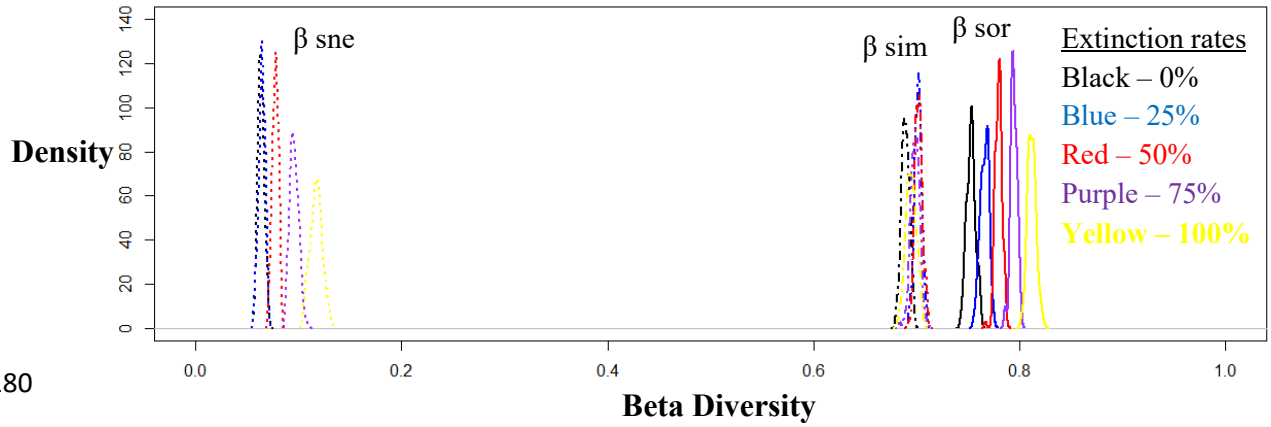
151 We measured the quality of the functional space used in our analysis, i.e. the best number
152 of coordinate axes, using the method proposed by Maire *et al.* (2015), considering the mean
153 square deviation (mSD) of the Euclidean distance (lower mSD represents higher quality in
154 functional space). Once we had both matrixes needed, the first step was to estimate the original
155 functional diversity indices among the seven basins, and then we randomly eliminated 25, 50%
156 and 75% from the total number of species from Doce Basin. In addition to the three random
157 extinction scenarios we measured the functional diversity without the species that are endemic
158 from Doce Basin. We also excluded from the functional matrix the species that were randomly
159 eliminated from the community matrix. For each scenario we then evaluated the shifts in
160 functional richness, measuring the possible changes occurred in the volume of multidimensional
161 space occupied by all species in Doce Basin within functional space. In this process we used the
162 methodology proposed by Mouillot *et al.* (2013) and Villéger *et al.* (2014), focusing in the
163 changes occurred at the level of functional richness.

164 **Results**

165 The seven basins summed 546 primary ray-finned fish species, with a highest richness in the
166 Grande Basin (292 species), followed by High São Francisco (166), Southern Paraíba (156),
167 Doce (139), ES coast (107), Jequitinhonha (92) and BA ES coast (84) (Figure 1). Doce Basin
168 had 15 exclusive species. Altogether, the number species exclusive from a single basin was 313,
169 evidencing the great importance of each basin to the regional species pool (gamma diversity).
170 The total β-div (β sor) increased, on average, from 0.751 (before the disaster) to 0.811 (total

171 extinction) (Fig. 2). The turnover component (β sim) contribution reduced from 87 (before the
172 disaster) to 81% (total extinction) of the total β-div. Meanwhile, the contribution of the
173 nestedness (β sne) increased from 13 (before the disaster) to 19% (total extinction) (Fig. 2).

174 For this case study, our simulations showed that after such environmental disturbance, the
175 increase of β-div was due mainly by the increase of the nestedness (Fig. 2). ANOVA showed
176 significant differences between all scenarios (p-value < 0; $p = 2e^{-16}$) (Fig. 3). Tukey Test showed
177 significant differences in all (p-values < 0.05), except one scenario: 0sne-1sne (p = 0.0562) (Fig.
178 3 A). Regardless the extinction level prompted by this environmental disturbance, significant
179 changes should have occurred at the β-div patterns (Fig. 3 C; p-values < 0.05).



180

181 **Figure 2**. Total dissimilarities comparisons between the five scenarios. Before the disaster
182 (black lines) and with 25% (blue lines), 50% (red lines), 75% (purple lines) and 100%
183 (yellow lines) of extinctions rates. Bsor – Sørensen dissimilarity (solid lines: total β-div).
184 Bsim – Simpson dissimilarity (dash-dot lines: turnover component of Sørensen
185 dissimilarity). Bsne – Nestedness (dot lines: nestedness component of Sørensen
186 dissimilarity).

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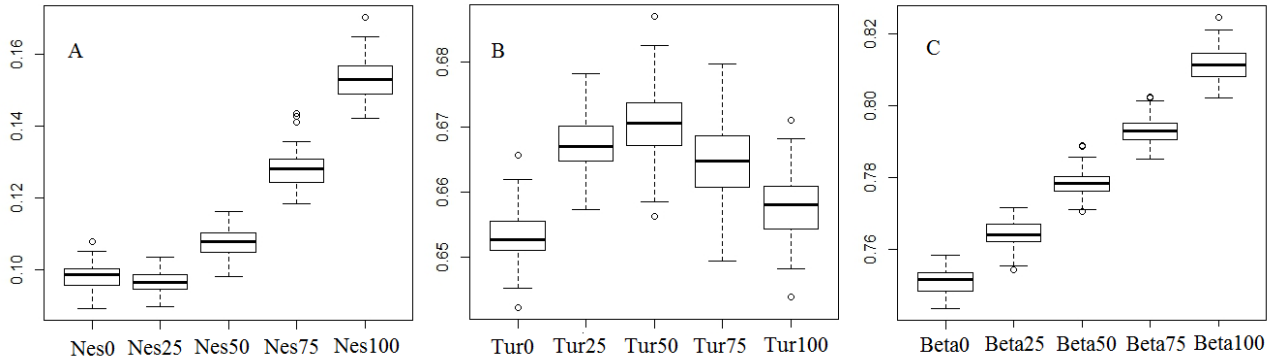

188

189 **Figure 3.** Comparisons among extinction scenarios in the three components of β-div: A -
190 nestedness, B - turnover, C - total β-div. Scenarios are represented by 0, 25, 50, 75 and 100% of
191 extinctions rates.

192

193 We used the first three functional coordinates axes to build the functional trait matrix,
194 with a quality functional space of mSD=0.0027. Among the seven basins analyzed in our
195 simulations, the basin that occupied most of the functional volume space before the disaster was
196 Grande Basin, with a convex hull volume of 91%, followed by Doce (69%, see Fig. 4 A), São
197 Francisco Alto (67%), Paraíba do Sul (65%), Litoral BA ES (56%), Jequitinhonha (55%) and
198 Litoral ES (55%). At the three levels of extinctions 25, 50 and 75%, the functional richness from
199 Doce Basin changed respectively to 55, 52 and 36% (Fig. 4 B, C, D). When only the species
200 exclusive to Doce Basin were excluded the functional richness decreased to 66% (Fig. 4 E).

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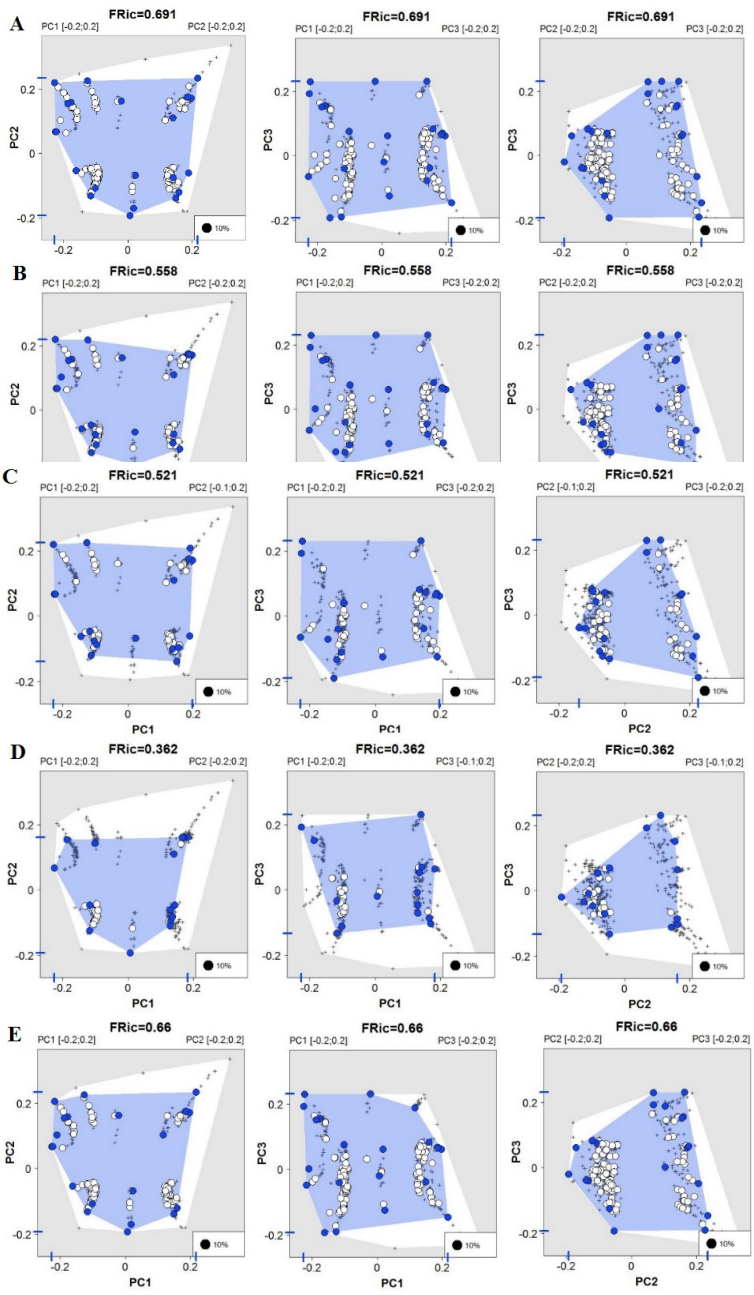

Figure 4. Shifts in functional richness: A- Original functional richness prior the Mariana disaster, B- 25% of random extinction, C- 50% of random extinction, D- 75% and E- scenario with the exclusive species from Doce Basin excluded (15 species). The white shapes represents 100% of the functional spaces occupied by all species presented in all basins and the blue shape represents the amount of functional spaces that the fish traits of each basin occupy. White and blue symbols are species being vertices in the multidimensional space.

Discussion

Biodiversity losses of primary ray-finned fishes from Doce Basin changed the amount of total β-div and direction of its components towards an increased contribution of nestedness. Systematic species loss from a given community will modify the patterns of regional β-div by decreasing the

contribution of turnover (subtractive homogeneization), those results are consistent with the findings of Toussaint *et al.* (2014). Functional richness also reduced in the patterns of the multidimensional functional space occupied by all species, which evidence that the likely depletion of functional richness is dependent on the position of each species in the functional space within a given community. The extirpation of the endemic species (15) from Doce Basin caused a loss of only 4.4% (Figure 4 E) from its total functional space occupied, indicating that those endemic species are functionally redundant (species with similar functional trait values). The other three extinction scenarios, 25, 50 and 75% decreased 20.2, 24.6 and 47.8% (Figure 4 B, C, D) respectively, which is slower than the reduction in species richness *per se*, thus in accordance with the high functional redundancy between communities.

The level of functional disturbances is highly dependent on the level of variations within functional traits presented by each species and also the magnitude/nature of the disaster itself. For the Mariana case study we considered that this havoc affected all biodiversity facets, without giving almost or any species the opportunity to withstand for survival. We supported our assumption by the fact that one of the most important parameter required by any primary ray-finned fishes is the level of the element salt in the water, e.g. primary freshwater fishes are those intolerant to a salinity level above 0.5 ‰ (Myers 1949). The Mariana disaster is known to have affected the Doce River with many heavy-metal elements (Fernandes *et al.* 2016), disrupting the quality of water required for fish survival. Another key factor that supports our assumption is the dissolved oxygen required for photosynthesis, respiration and other biological end ecological processes. When a massive quantity of biological agents perish into the freshwater environment the decomposing process of the organic matter consumes high amounts of dissolved oxygen, suffocating to die any fish species (Costa & Barletta 2016).

Taxonomic β-div and functional richness approaches are able to give deep insights about the structure and possible changes in biodiversity variations. Our analysis showed that, despite any level of extinction, the patterns of taxonomic β-div suffered significant variations (Figure 2), and the increased contribution of nestedness to the total β-div evidenced the importance of all local diversities (alpha diversity) to the set pool of regional diversity (gamma diversity). The Mariana disaster may have permanently affected all aspects of biodiversity from that region, and those variations certainty were spreader among other taxa. Simulations with empirical β-div and functional richness data are a handy tool of analysis to predict and assess the consequences of anthropocentric or natural disturbances in space and time.

As we enter in the Antropocene epoch, we withstand harsh biological losses (WWF 2016), mainly in the freshwater realm (Costa & Barletta 2016, Dudgeon *et al.* 2006). The core challenge for ecological scientists, natural resources managers and stakeholders is to comprehend how we are shifting all biodiversity facets (taxonomic, functional and phylogeny diversities) over space and time (Cardoso *et al.* 2014, Cianciaruso *et al.* 2012, Magurran *et al.* 2010). The Mariana disaster represents one sad aspect of the Antropocene, where the natural resources are exploited even at the cost of human lives and extreme biodiversity losses. Given the utmost importance of the ecosystem services provided by freshwater ecosystems, such as subsistence fisheries, for food security in many fishing communities across the globe (McIntyre *et al.* 2016), such abrupt havocs transcend economic, cultural and environmental barriers.

References

ANA, 2015. *Agência Nacional de Águas. Ministério do Meio Ambiente*. (Accessed on 04 2015). Available from http://www2.ana.gov.br/Paginas/default.aspx

273 Baselga A, 2010. Partitioning the turnover and nestedness components of beta diversity. *Global*
274 *Ecology and Biogeography*, 19: 134-143.
275 Baselga A & Orme CDL, 2012. betapart: an R package for the study of beta diversity. *Methods*
276 *in Ecology and Evolution*, 3: 808-812.
277 Burkhead NM, 2012. Extinction rates in North American freshwater fishes, 1900–2010.
278 *BioScience*, 62: 798-808.
279 Cardoso P, Rigal F, Carvalho JC, Fortelius M, Borges PA, Podani J *et al.*, 2014. Partitioning
280 taxon, phylogenetic and functional beta diversity into replacement and richness difference
281 components. *Journal of Biogeography*, 41: 749-761.
282 Cianciaruso MV, Silva IA, Batalha MA, Gaston KJ & Petchey OL, 2012. The influence of fire
283 on phylogenetic and functional structure of woody savannas: moving from species to individuals.
284 *Perspectives in Plant Ecology, Evolution and Systematics*, 14: 205-216.
285 Costa M & Barletta M, 2016. Special challenges in the conservation of fishes and aquatic
286 environments of South America. *Journal of fish biology*.
287 Dornelas M, Magurran AE, Buckland ST, Chao A, Chazdon RL, Colwell RK *et al.*, 2013.
288 *Quantifying temporal change in biodiversity: challenges and opportunities*. Proc. R. Soc. B: The
289 Royal Society, p. 20121931
290 Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C *et al.*, 2006.
291 Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological*
292 *reviews*, 81: 163-182.
293 Escobar H, 2015. Mud tsunami wreaks ecological havoc in Brazil. *Science*, 350: 1138-1139.

294 Fernandes GW, Goulart FF, Ranieri BD, Coelho MS, Dales K, Boesche N *et al.*, 2016. Deep into
295 the mud: ecological and socio-economic impacts of the dam breach in Mariana, Brazil. *Natureza*
296 *& Conservação*, 14: 35-45.
297 Froese R & Pauly D, 2017. *FishBase*. (Accessed on January 2017). Available from
298 www.fishbase.org
299 IUCN, 2015. *The IUCN Red List of Threatened Species*. (Accessed on November 2015).
300 Available from http://www.iucnredlist.org
301 Magurran AE, 2016. How ecosystems change. *Science*, 351: 448-449.
302 Magurran AE, Baillie SR, Buckland ST, Dick JM, Elston DA, Scott EM *et al.*, 2010. Long-term
303 datasets in biodiversity research and monitoring: assessing change in ecological communities
304 through time. *Trends in ecology & evolution*, 25: 574-582.
305 Maire E, Grenouillet G, Brosse S & Villéger S, 2015. How many dimensions are needed to
306 accurately assess functional diversity? A pragmatic approach for assessing the quality of
307 functional spaces. *Global Ecology and Biogeography*, 24: 728-740.
308 Mason NW, Mouillot D, Lee WG & Wilson JB, 2005. Functional richness, functional evenness
309 and functional divergence: the primary components of functional diversity. *Oikos*, 111: 112-118.
310 McGill BJ, Dornelas M, Gotelli NJ & Magurran AE, 2015. Fifteen forms of biodiversity trend in
311 the Anthropocene. *Trends in ecology & evolution*, 30: 104-113.
312 McIntyre PB, Liermann CAR & Revenga C, 2016. Linking freshwater fishery management to
313 global food security and biodiversity conservation. *Proceedings of the National Academy of*
314 *Sciences*: 201521540.

315 Melo AS, Schneck F, Hepp LU, Simões NR, Siqueira T & Bini LM, 2011. Focusing on
316 variation: methods and applications of the concept of beta diversity in aquatic ecosystems. *Acta*
317 *Limnologica Brasiliensia*, 23: 318-331.
318 Mouillot D, Graham NA, Villéger S, Mason NW & Bellwood DR, 2013. A functional approach
319 reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28: 167-177.
320 Myers GS, 1949. Salt-tolerance of fresh-water fish groups in relation to zoogeographical
321 problems. *Bijdragen tot de Dierkunde*, 28: 315-322.
322 Pantanowitz A & Marwala T, 2009. Missing data imputation through the use of the Random
323 Forest Algorithm. *Advances in Computational Intelligence*, Springer, p. 53-62.
324 Pauly D, 1986. A simple method for estimating the food consumption of fish populations from
325 growth data and food conversion experiments. *Fishery Bulletin*, 84: 827-840.
326 Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM *et al.*, 2014.
327 Imputation of missing data in life-history trait datasets: which approach performs the best?
328 *Methods in Ecology and Evolution*, 5: 961-970.
329 R Core Team, 2016. *R: A language and environment for statistical computing. R Foundation for*
330 *Statistical Computing, Vienna, Austria.* 2014). Available from http://www.R-project.org/.
331 Socolar JB, Gilroy JJ, Kunin WE & Edwards DP, 2016. How should beta-diversity inform
332 biodiversity conservation? *Trends in ecology & evolution*, 31: 67-80.
333 Stekhoven DJ & Bühlmann P, 2012. MissForest—non-parametric missing value imputation for
334 mixed-type data. *Bioinformatics*, 28: 112-118.
335 Toussaint A, Beauchard O, Oberdorff T, Brosse S & Villéger S, 2014. Historical assemblage
336 distinctiveness and the introduction of widespread non-native species explain worldwide changes
337 in freshwater fish taxonomic dissimilarity. *Global Ecology and Biogeography*, 23: 574-584.

338 Villéger S, Mason NW & Mouillot D, 2008. New multidimensional functional diversity indices
339 for a multifaceted framework in functional ecology. *Ecology*, 89: 2290-2301.
340 Villéger S, Grenouillet G & Brosse S, 2013. Decomposing functional β-diversity reveals that low
341 functional β-diversity is driven by low functional turnover in European fish assemblages. *Global*
342 *Ecology and Biogeography*, 22: 671-681.
343 Villéger S, Grenouillet G & Brosse S, 2014. Functional homogenization exceeds taxonomic
344 homogenization among European fish assemblages. *Global Ecology and Biogeography*, 23:
345 1450-1460.
346 Villéger S, Miranda JR, Hernández DF & Mouillot D, 2010. Contrasting changes in taxonomic
347 vs. functional diversity of tropical fish communities after habitat degradation. *Ecological*
348 *Applications*, 20: 1512-1522.
349 WWF. 2016. Living Planet Report 2016. Risk and resilience in a new era. WWF International,
350 Gland, Switzerland. Report no.

351